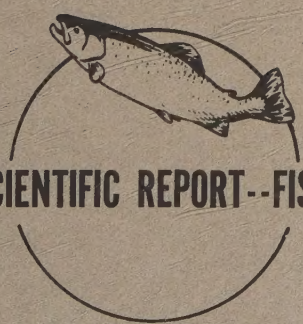
The Response of Tuna and Other Fish To Electrical Stimuli



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United States Department of the Interior, Fred A. Seaton, Secretary
Fish and Wildlife Service

THE RESPONSE OF TUNA AND OTHER FISH TO ELECTRICAL STIMULI

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ABSTRACT

Theoretical studies are presented of the potential, electric field, and current density for spherical electrodes submerged in a large body of water. The problem of the relationship between the head-to-tail potential and current density in a fish as determined by the relative conductivities of the fish and water is also investigated.

Preliminary experiments with aholehole (Kuhlia sandvicensis) are described in which were sought the optimum values of current density, pulse frequency, and pulse duration for electrotaxis in a small tank. These were found to be 6.6 ma./cm.^{2}, 10 c.p.s., and 6 to 8 milliseconds respectively.

A capacitor discharge apparatus was constructed for use with tuna in a large tank. With this apparatus it was possible to induce electrotaxis in small (50 cm.) yellowfin tuna using a pulse frequency of 20 c.p.s. and current density of 4.0 ma./cm.^{2}.

CONTENTS

Page

Introduction 1

Electric field in a conducting medium 1

The fish in a uniform electric field 1

Preliminary experiments with aholehole 2

Apparatus 3

Procedure and results 4

Discussion 7

Experiments with tuna and other large fish 8

Apparatus 8

Procedure and results 11

Discussion 12

Summary 14

Literature cited 14

Appendix I - The electric field in a conducting medium 16

The potential 17

The electric field 19

The current density 19

Resistance 20

Discussion 20

Appendix II - A fish in a uniform electric field 21

Head-to-tail potential 22

Current density 23

ILLUSTRATIONS

FIGURE Page

1. Schematic diagram of apparatus used in experiments with aholehole. 3

2. Pulse shapes. A. Nearly square wave used in experiments with aholehole. B. Wave of capacitor discharge used in experiments with tuna and other large pelagic fish; and equivalent square wave. 4

3. Relationship between total peak current (I) for satisfactory response and length of fish (L). Dashed line expresses the relationship I = 176/L. 6

4. The capacitor discharge circuit. A. Schematic diagram of complete system. B. Bank of fifty-five 1,000 mfd. capacitors. 10

5. The mechanical interrupter. A. General view showing variable speed motor, contactor (one is removed), and drive cams. B. Close-up view of spring-loaded contactor. . . . 11

6. Power dissipation per unit volume of water vs. pulse frequency for satisfactory response in tuna. 13

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One of the most efficient methods of harvesting tuna is live-bait fishing in which the tuna are attracted and held near the vessel by chumming with small, live-bait fish and are caught by pole and line with artificial lures or "jigs." Unfortunately, in Hawaii and elsewhere in the Pacific, the supplies of baitfish are limited in abundance and distribution and this fact in turn limits the catch of existing fisheries and curtails the development of new ones. A method of directing the fish to the vessel and holding them by electrical compulsion could eliminate to a large extent the need for live bait and would simplify the fishing operation in other respects as well.

The present study, undertaken during 1954 and 1955 under Contract Nos. 14-19-008-2204 and 14-19-008-2317 between the University of Hawaii and the Pacific Oceanic Fishery Investigations of the Fish and Wildlife Service, is concerned with some of the technical problems involved in electrofishing in sea water and particularly with the power requirements necessary to elicit electrotaxis in tuna. It includes theoretical studies on the distribution of the electric field in a highly conductive medium such as sea water and on the internal and external fields affecting a fish. It also includes preliminary studies on a small marine fish, the aholehole, or mountain bass (Kuhlia sandvicensis), to determine optimum values of current density, pulse duration and pulse frequency for electrotaxis in a small tank. It describes an apparatus designed to produce electrotaxis in tuna in a large tank and provides the results of experiments which show that tuna exhibit the electrotactic response. Finally it includes a discussion of the power requirements in the open sea as compared with those in a small tank.

ELECTRIC FIELD IN A CONDUCTING MEDIUM

In any attempt at electrofishing in sea water one is faced with the high conductivity of sea water and the consequent large dissipation of energy which taxes the source of power. Although Cattley (1955a) indicates that the theoretical field in a conducting medium is known, we have been unable to locate a description in the literature. Consequently, the junior author investigated the theoretical field between two spherical electrodes and arrived at the mathematical solution given in detail in Appendix I.

In summary, for spherical electrodes deeply submerged in a large body of water, formulae are presented for calculating at any point in the medium the potential (V), the electric field ($\vec{E}$), and the current density ($\vec{J}$). The total current (I) between two such electrodes is given by

$$I = 4\pi \sigma a V \text{ amperes}$$

and the net resistance (R) is given by

$$R = 1/(2\pi\sigma a) \text{ ohms}$$

where σ is the conductivity of the water in $(\text{ohm-cm.})^{-1}$,
a is the radius of the electrodes in cm., and
V is the potential applied to the electrodes in volts.

It will be noted that the total current is independent of the distance between the electrodes. This agrees with the statement by Cattley (1955a) that "...the current passing will not decrease appreciably when electrodes 10 or more meters apart are further separated..." except that there are no limitations in the theoretical model.

THE FISH IN A UNIFORM ELECTRIC FIELD

Cattley (1955b) has discussed the response of a fish in a uniform, conducting medium which is (a) of the same resistance as the body of the fish, (b) of less resistance than the fish, and (c) of greater resistance than the fish for a specimen

of such size that a head-to-tail difference in potential of 1 volt will cause the fish to swim to the anode in medium (a). He points out that in fresh water, presuming the resistance of the fish is less than that of the medium, the equipotential surfaces will diverge in the vicinity of the fish, requiring a greater potential gradient to elicit response than in (a); however in salt water, presuming the resistance of the fish is greater than the medium, the equipotential surfaces will converge in the vicinity of the fish, requiring a smaller potential gradient to elicit response than in (a). He thus concludes that the "...voltage gradients need not be so great /in salt water/ as in fresh water..."

This problem was approached independently by the junior author before seeing Cattley's (1955b) paper. Particularly, it was desired to determine the head-to-tail potential in the fish and the current passing through the fish when immersed in fresh and salt water with a uniform electric field. The theoretical approach is given in detail in Appendix II. To simplify the mathematics, it has been assumed that the fish forms a sphere. Thus, the formulae which have been developed must be regarded as approximations when applied to a fish which, of course, differs considerably in shape from a sphere. They indicate in a qualitative way, however, the results that can be expected with an organism such as a fish.

In summary, it is concluded that the head-to-tail voltage of this theoretical spherical fish (V_L volts) may be expressed as

$$V_L = E_o L \frac{3\sigma_w}{\sigma_f + 2\sigma_w}$$

Where E_o is the uniform electric field (volts/cm.),
L is the length of the fish (cm.),
σ_w is the conductivity of the water (ohm-cm.)$^{-1}$, and
σ_f is the conductivity of the fish (ohm-cm.)$^{-1}$.

When the conductivity of the fish is greater than that of the medium, as it may be in some fresh waters, the head-to-tail voltage is less than $E_o L$; when the conductivity of the fish is less than the medium, as in salt water, the head-to-tail voltage is greater than $E_o L$. With reasonable assumptions as to the relative conductivities of sea water, fresh water and the fish, it is concluded that for a fish of a given size, the electric field intensity in sea water would need to be about 1/10 as large as in fresh water to elicit an equivalent response. It is also shown that the current density in the fish (J_f) is a constant (σ_f/L) times the head-to-tail potential:

$$J_f = \left(\frac{\sigma_f}{L}\right) V_L$$

Thus, neither current density nor potential, individually, can be said to be responsible for electrically produced responses of the fish.

The above results are in general agreement with the unsupported discussions of Cattley (1955b) who intimates that the field in sea water would need to be about 1/6 to 1/12 or, again, roughly 1/10 that of fresh water. His comparison, however, is given in terms of relative power requirements.

PRELIMINARY EXPERIMENTS WITH AHOLEHOLE

Morgan (1953) initiated experiments during 1950 at the University of Hawaii to study the response of the aholehole, a tropical marine fish, to interrupted direct current in sea water. Using a wooden tank 12 x 2 x 2 feet, a mechanical current interrupter, and a 5 kw. direct current motor-generator, he showed that an interruption frequency of 15 cycles per second (c.p.s.) gave more positive response than frequencies of 5 and 20 c.p.s. and that equivalent response could be obtained by progressively decreasing the "on-fraction" of a cycle from 0.75 to 0.25. Although the peak current remained about the same, the average current was considerably lower at the smallest on-fraction, thus achieving a net saving of power.

Using the same tank and generator, but galvanized iron plate rather than carbon pencil electrodes, Tester (1952) showed that at 15 c.p.s. the on-fraction could be reduced to about 0.08, with a further net saving of power.

The above results are in agreement with those of Dr. Konrad Kreutzer of Germany (Houston 1949) in indicating the desirability of using a short "on-fraction." Kreutzer indicated that the pulse duration should be from 1 to 5 milliseconds (on-fraction 0.015 to 0.075 at 15 c.p.s.) and that the frequency should be from 4 to 60 c.p.s. depending on the natural swimming frequency of the fish.

Neither Morgan nor Tester discussed the shape of the pulse, although it was found on an oscilloscope to be peaked. According to Cattley (1955c), Kreutzer has emphasized the importance of the pulse which in his apparatus is the discharge from a capacitor with a sharp rise from zero followed by a much slower decay. Groody, Loukashkin and Grant (1952) at first believed that the sawtooth or the 1/4-sine wave gave the best response in sardines, but later Loukashkin

and Grant (1954), concluded that a variety of wave shapes gave satisfactory control of the fish. However, they found that wave shape exerted an influence on the speed and smoothness of movement with either continuous or interrupted half wave rectified 60-cycle alternating current being the most effective and "satisfactory." They also found that capacitor discharge produced "satisfactory" reactions at very low average current densities (0.4 to 0.8 milliamperes per square inch) thus representing a substantial decrease in power requirements.

It was decided to continue the experiments of Morgan (1953) and Tester (1952) to determine for aholehole the optimum on-fraction and minimum power requirements for satisfactory response. It was planned to use these results as a basis for calculating the necessary characteristics of an apparatus designed to produce electrotaxis in tuna in a much larger tank.

Apparatus

The tank (12 x 2 x 2 feet) was the same as that used by Morgan (1953) but was lined with fiberglass cloth impregnated with synthetic resin. Fresh sea water, flowing continuously into one end of the tank and out the other, was held at a constant depth of 12 inches by means of a float valve attached to the outlet. The temperature of the water varied from 26° to 28°C.

Electrodes made of 1/2-inch mesh, galvanized, iron hardware cloth and measuring 24 x 24 inches were placed vertically at each end of the tank. The distance between the electrodes was 10 feet. Plastic screens were inserted 12 inches from each electrode to prevent the fish from coming into contact with the electrodes. Batteries, mechanical interrupter, rheostat, ammeter, and a reversing switch made up the rest of the equipment. The schematic diagram is shown in figure 1.

Automobile storage batteries were used rather than a d.c. generator in order to reduce the inductance effect which causes arcing at the interrupter contacts and a distorted wave form. Eleven batteries were necessary to obtain the highest current densities required.

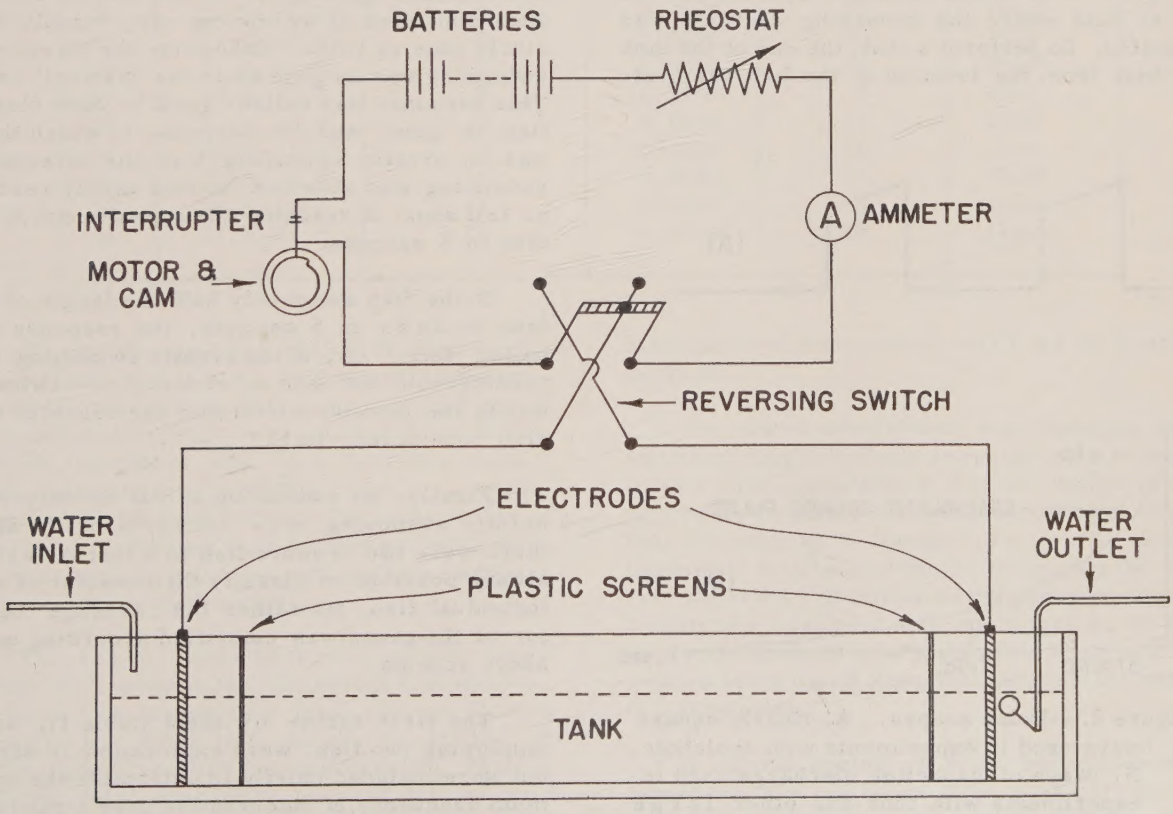


Figure 1.--Schematic diagram of apparatus used in experiments with aholehole.

The mechanical interrupter consisted of a motor-driven cam operating a spring-loaded contact point. The cam consisted of eight identical lamina so that the pitch of the cam and hence the on-fraction was controlled by the rotations of the lamina relative to each other. When the lamina were all lined up, the on-fraction was 0.02. The pulse recurrence frequency was controlled by a variable speed drive between the motor and cam.

Since the electrodes completely covered one end of the tank it was expected that the current density and hence the electric field would be uniform throughout the cross-section of the tank. Measurements confirmed that this was so.

The wave shape was checked by means of an oscilloscope connected across the electrodes and was found to deviate slightly from a square wave. The top plateau sloped slightly downward as shown in figure 2A.

Procedure and Results

During the first series of tests two fish were in the tank during each test. In following series, four fish were used. The fish, when not being shocked, tended to stay away from the end of the tank where the reversing switch was operated. To perform a test, the end of the tank farthest from the location of the fish was made positive for 5 seconds and then the polarity was reversed for another 5 seconds. Observations of the fish's behavior were then recorded along with the lengths of the fish, the total peak current producing the shock, the pulse frequency, the on-fraction, and the water temperature. The total peak current was the total current flowing through the tank when the interrupter contacts were closed.

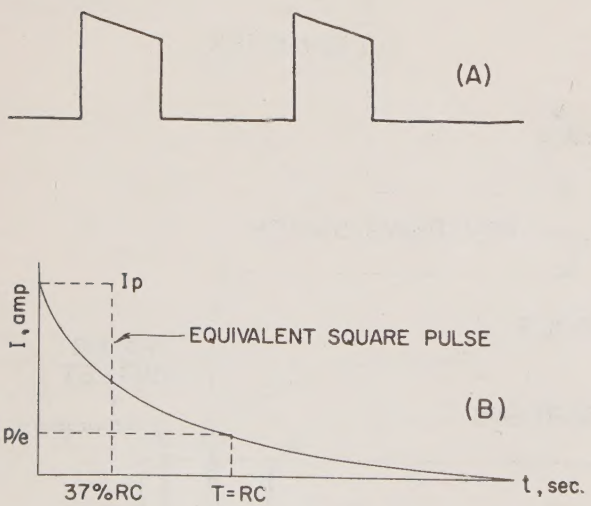


Figure 2.--Pulse shapes. A. Nearly square wave used in experiments with aholehole. B. Wave of capacitor discharge used in experiments with tuna and other large pelagic fish; and equivalent square wave (for explanation see text).

It was difficult to classify the fish behavior into a fixed group of categories, but the following classification was used. A "perfect" response was one in which the fish immediately oriented itself and swam directly and rapidly towards the positive electrode when the current was turned on. When arriving at the protective barrier, the fish continued to swim against the barrier until the current was turned off. Upon reversal of the current, the fish immediately turned about and swam towards the opposite end as before. The fish, in a "perfect" response condition, easily reached the opposite end of the tank in less than 5 seconds.

Such perfect response was not frequently encountered. Very frequently the fish would behave erratically either at the instant the switch was closed or when it reached the barrier screen. This consisted of swimming very rapidly in a circle once or twice. Otherwise the directional swimming was as good as in the "perfect" case. This response was called "good." Also classified as "good" was the response in which there was no erratic swimming but the directional swimming was slow and the fish barely reached or fell short of reaching the opposite end of the tank in 5 seconds.

If the fish swam only half the length of the tank or less in 5 seconds, the response was called "fair." Or, if the erratic swimming was considerable but with a tendency to swim towards the positive electrode, the behavior was also considered "fair."

Finally, no swimming at all or only very erratic swimming was called "poor." Since there were two or more fish in a test it was not always possible to classify the behavior of each individual fish, but rather the "average" behavior of the group was classified according to the above scheme.

The first series of tests (table 1), each employing two fish, were exploratory in nature but were designed chiefly to determine the optimum frequency of interruption over a range of on-fractions. Disregarding on-fraction, a "satisfactory" response (either "perfect" or

Table 1.--Minimum total peak current for electrotactic response of aholehole at various "on-fractions" and frequencies

Exp. No.	Fish length, cm.	Total peak current, amp.	On-fraction	Pulse rate, c.p.s.	Response
1	11.5; 12.5	8	0.1333	15	Good
2	11.5; 12.5	8	0.1333	10	Poor
3	12.5; 13.2	8	0.1333	5	Fair
4	12.5; 13.2	8	0.1333	10	Good
5	12.5; 13.2	8	0.0695	10	Perfect
6	12.5; 13.2	8	0.0695	5	Good
7	12.5; 13.2	8	0.0695	15	Poor
8	11.3; 11.7	8	0.0444	5	Poor
9	11.3; 11.5	8	0.0444	10	Poor
10	11.3; 11.5	9	0.0444	15	Poor
11	11.5; 12.0	9	0.0444	5	Poor
12	11.5; 12.0	10	0.0444	10	Perfect
13	11.3	10	0.0444	10	Perfect
14	12.5; 13.5	8	0.0444	5	Good
15	12.2; 12.5	8	0.0333	10	Good
16	12.2; 12.5	8	0.0333	5	Poor
17	12.2; 12.5	9	0.0333	15	Fair
18	12.2; 12.5	8	0.0333	10	Fair
19	12.3; 12.6	8	0.0333	5	Fair
20	12.3; 12.6	8	0.0333	15	Fair
21	12.3; 12.6	10	0.0333	10	Good
22	11.3; 12.0	8	0.0200	10	Perfect
23	11.3; 12.2	8	0.0200	5	Fair
24	11.3; 12.2	8	0.0200	15	Good
25	11.3; 12.2	8	0.0200	10	Fair
26	11.5; 12.2	8	0.0200	10	Poor
27	11.5; 12.2	8	0.0200	5	Fair
28	11.5; 12.2	8	0.0200	15	Fair
29	11.5; 12.2	9	0.0200	10	Fair
30	11.5; 12.2	11	0.0200	10	Good
31	11.5; 12.2	11	0.0200	5	Poor
32	11.5; 12.2	12	0.0200	10	Good

"good") was obtained in 2 out of 10 experiments (20 percent) at 5 c.p.s., in 9 out of 15 experiments (60 percent) at 10 c.p.s., and in 2 out of 7 experiments (29 percent) at 15 c.p.s. It was decided, therefore, that 10 c.p.s. was closer to the optimum frequency than 15 c.p.s. as determined by Morgan (1953). The first series of tests also indicated that a greater total peak current was required for satisfactory response at the smaller on-fractions.

The term "total peak current" is used rather frequently in the discussion that follows. By "total" is meant the total current flowing through the water between the electrodes, as distinguished from the current density. Table 5 converts total current to current density and electric field intensity. By "peak" is meant the value of the current at the peak of the pulse as distinguished from some sort of an average current.

The above conclusions are tentative as it was exceedingly difficult to appraise the response in this quasi-quantitative manner and as it was necessary to utilize the same fish several times, thus introducing a "fatigue" factor. It seems likely that this fatigue factor increased the current necessary to elicit satisfactory response. Sometimes a fatigued fish would turn on its side in a state of electronarcosis when a current was applied which would otherwise induce electrotaxis in a fresh fish.

A second series of tests was designed to determine the minimum total peak current for satisfactory response at a constant frequency of 10 c.p.s. at each of the following on-fractions:

Table 2.--Minimum total peak current for satisfactory electrotactic response of aholehole at various "on-fractions" with a constant frequency of 10 c.p.s.

Exp. No.	Fish length, cm.	Total peak current, amp.	On-fraction	Response
1	12.1; 12.6; 13.2; 13.4	16	0.02	Fair
2	11.0; 11.3; 11.3; 11.7	14	0.04	Good
3	11.2; 11.5; 11.7; 12.2	12	0.06	Good
4	11.2; 11.3; 11.7; 11.7	12	0.08	Good
5	11.2; 11.3; 11.7; 11.7	16	0.12	Perfect
6	11.4; 11.4; 11.5; 11.6	14	0.16	Good

0.02, 0.04, 0.06, 0.08, 0.12, and 0.16. For each on-fraction the same 4 fish were used in several successive trials at increasing currents of 6, 8, 10, 12, 14, and 16 amp. Table 2 shows the minimum total peak current for satisfactory response. Again it was difficult to distinguish between shades of satisfactory response at some of the higher currents and the results were doubtful in some cases because of the fatigue factor. It was tentatively concluded, however, that the minimum current for satisfactory response (12 amp.) was associated with an on-fraction of 0.06 to 0.08.

In a third series of tests, each employing two fish with the results shown in table 3, an attempt was made to determine the relationship between peak current for satisfactory response and length of fish for a constant on-fraction of 0.08 and a frequency of 10 c.p.s. Unfortunately only a small range of fish sizes were available. However, the results plotted in figure 3 indicate that the total peak current requirement decreases with increase in fish length. If we assume a simple reciprocal relationship $I=k/L$ and if we choose k so this equation fits our data at L = 11 cm. and I = 16 amp., the curve shown as a dashed line in figure 3 results. Although the curve does not fit the data well, it is perhaps realistic in that the curve must ultimately approach the horizontal.

In a fourth and final series of tests, at an on-fraction of 0.06, and a frequency of 10 c.p.s., the total peak current was adjusted to the optimum value according to the length of the fish. As shown in table 4 all tests resulted in satisfactory response except No. 4, which was made on a school of 29 fish varying in length from 9 to 12 cm. When the current was adjusted to the longer fish, there was considerable erratic swimming by the shorter fish which tended to interfere with the electrotactic response of the longer fish. However, the school as a whole moved slowly towards the positive electrode. When the schools were of more nearly uniform size as in

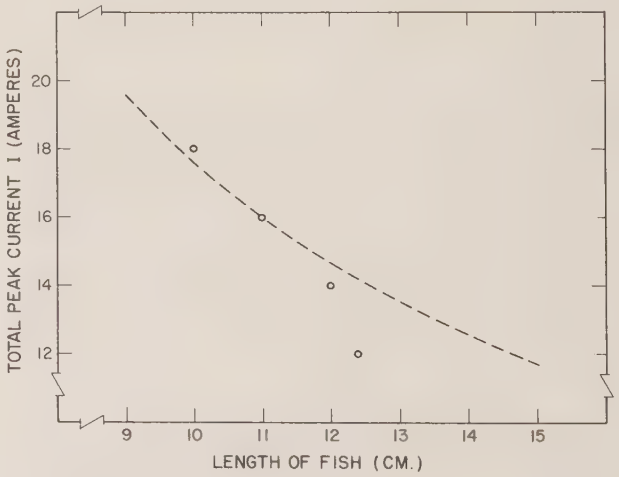


Figure 3.--Relationship between total peak current (I) for satisfactory response and length of fish (L). Dashed line expresses the relationship I = 176/L.

Table 3.--Electrotactic response of aholehole of various size groups to increasing current at a constant "on-fraction" of 0.08 and a frequency of 10 c.p.s.

Exp. No.	Fish length, cm.	Total peak current, amp.	Response
1a	12.4; 12.4	6	Poor
b	12.4; 12.4	8	Poor
c	12.4; 12.4	10	Fair
d	12.4; 12.4	12	Perfect
2a	11.0; 11.0	6	Poor
b	11.0; 11.0	8	Poor
c	11.0; 11.0	10	Poor
d	11.0; 11.0	12	Fair
e	11.0; 11.0	14	Fair
f	11.0; 11.0	16	Good
3a	10.0; 10.1	6	Poor
b	10.0; 10.1	8	Poor
c	10.0; 10.1	10	Poor
d	10.0; 10.1	12	Poor
e	10.0; 10.1	14	Fair
f	10.0; 10.1	16	Fair
g	10.0; 10.1	18	Good
4a	11.9; 12.1	6	Poor
b	11.9; 12.1	8	Fair
c	11.9; 12.1	10	Fair
d	11.9; 12.1	12	Good
e	11.9; 12.1	14	Perfect

tests 5 and 6, there was much less confusion and the school as a whole swam rapidly towards the positive electrode.

Discussion

In the foregoing experiments only the total peak current, I, was measured and recorded. This quantity was also used in the tables and graphs. The current density is, of course, the more significant factor and it is related to the total current by $J = I/A$, where J is the peak current density and A is the cross-sectional area of the column of water between the electrodes. In table 5 the current densities corresponding to the currents used in the experiments are listed.

The resistance between the electrodes was found by measuring the voltage between the electrodes for a given current. Then $R = V/I$, where R is the resistance in ohms, V the voltage in volts, and I the current in amperes. The resistivity of the sea water can then be found by the standard formula $\rho = RA/L$, where ρ is the resistivity, R the resistance, A the cross-section

Table 4.--Response of aholehole to the predicted optimum current. Pulse frequency: 10 c.p.s.; on-fraction: 0.06

Exp. No.	Number of fish	Fish length, cm.	Total peak current, amp.	Response
1	2	12.0; 12.5	12	Good
2	2	11.3; 11.4	14	Perfect
3	2	10.3; 10.3	18	Good
4	29	9 to 12	14	Fair
5	29	av. 10.4	16	Good
6	10	av. 9.5	19	Perfect

Table 5.--The relationship between total current, current density, and electric field

Total current (I), amp.	Current density (J), ma./cm.^{2}	Electric field (E), volts/cm.
4.0	2.2	0.041
4.5	2.5	0.046
5.0	2.8	0.051
5.5	3.0	0.057
6.0	3.3	0.062
6.5	3.6	0.067
7.0	3.9	0.072
7.5	4.1	0.077
8.0	4.4	0.082
9.0	5.0	0.093
10.0	5.5	0.10
11.0	6.1	0.11
12.0	6.6	0.12
13.0	7.2	0.13
14.0	7.7	0.14
16.0	8.8	0.16
18.0	9.9	0.19
20.0	11.0	0.21

area of the column of water between the electrodes, and L the length of the column. These calculations gave for ρ a value of 18.68 ohm-cm. As would be expected, this is smaller than the value of the resistivity of sea water on the west coast of the United States (about 29.5 ohm-cm.), where both the temperature and salinity are lower.

The electric field established in the water is related to the current density by $E = \rho J$, where E is the electric field in volts/cm., ρ the resistivity in ohm-cm., and J the current density in amperes/cm.^{2}. The values of the electric field corresponding to the various values of current used in the experiment are listed in table 5.

The approximate head-to-tail voltages for satisfactory response, calculated as the product of electric field intensity and length of fish, varied between 1 and 2 volts in these tests.

EXPERIMENTS WITH TUNA AND OTHER LARGE FISH

It has been shown by Tester (1952) that tuna may be successfully kept in captivity in a large concrete tank (35 x 11 x 4 feet) located at the Hawaii Marine Laboratory, Coconut Island, Oahu. Our problem was to design an apparatus which would produce an electric field of sufficient strength to induce electrotaxis in tuna in this relatively large volume of water (ca. 10,000 gals.).

Apparatus

Preliminary experiments on aholehole in a small tank, described in the preceding section, showed that satisfactory electrotaxis could be induced with a frequency of 10 c.p.s., with an on-fraction of about 0.06 and with a peak current density of 8.8 ma./cm.^{2} (for an 11-cm. fish). Although admittedly tenuous, the frequency was assumed to be optimal for best directional swimming and the on-fraction was assumed to be optimal for minimum power requirement. The combination of frequency and on-fraction corresponds with a pulse duration of 6 milliseconds. The peak current corresponds with an electric field of 0.16 volts/cm. (table 5). If it is assumed that the electric field (E) for satisfactory response varies with the length of the fish (L) according to the rough relationship $E = k/L$, k (a proportionality constant) may be calculated at 1.8 volts and the minimum field requirement is

$$E = \frac{1.8}{L} \text{ volts/cm.}$$

With the further and perhaps questionable assumption that k will be the same for aholehole and tuna, the electric field necessary to induce satisfactory electrotaxis in a 30-cm. tuna may be calculated at E = 0.060 volts/cm. The

corresponding current density (J) at a resistivity (ρ) of 18.68 ohm-cm. is $J = E/\rho = 0.0032$ amp./cm.^{2}. For a tank of cross section 11 x 4 feet, the total current (JA) will then be 130 amp. This is, of course, the total peak current during an on-period. Assuming the electrodes will be spaced a distance (ℓ) of 33 feet, the voltage between electrodes will be $E\ell = 60$ volts. As the experiments were to be conducted on tuna and other fish greater than 30 cm. in length, a current of about 130 amperes at a potential of about 60 volts was considered the maximum requirement. As this current will be "on" for only 6 percent of the time, the power requirement is a modest 470 watts.

Unfortunately a current as large as 130 amperes cannot be handled as simply as that of the 18-ampere maximum in the preliminary experiments. A major problem is arcing at the contacts on breaking the circuit; a less serious problem is obtaining a current source of this magnitude. These difficulties can be overcome by charging and discharging capacitors, a principle employed by Kreutzer and Peglow (Cattley 1955b).

A schematic diagram of a system utilizing capacitor discharge is shown in figure 4A. Initially contactor No. 1 is closed and No. 2 open, thus charging the capacitor to a voltage approaching that of the source. Then contactor No. 1 opens and No. 2 closes, discharging the capacitor through the tank.

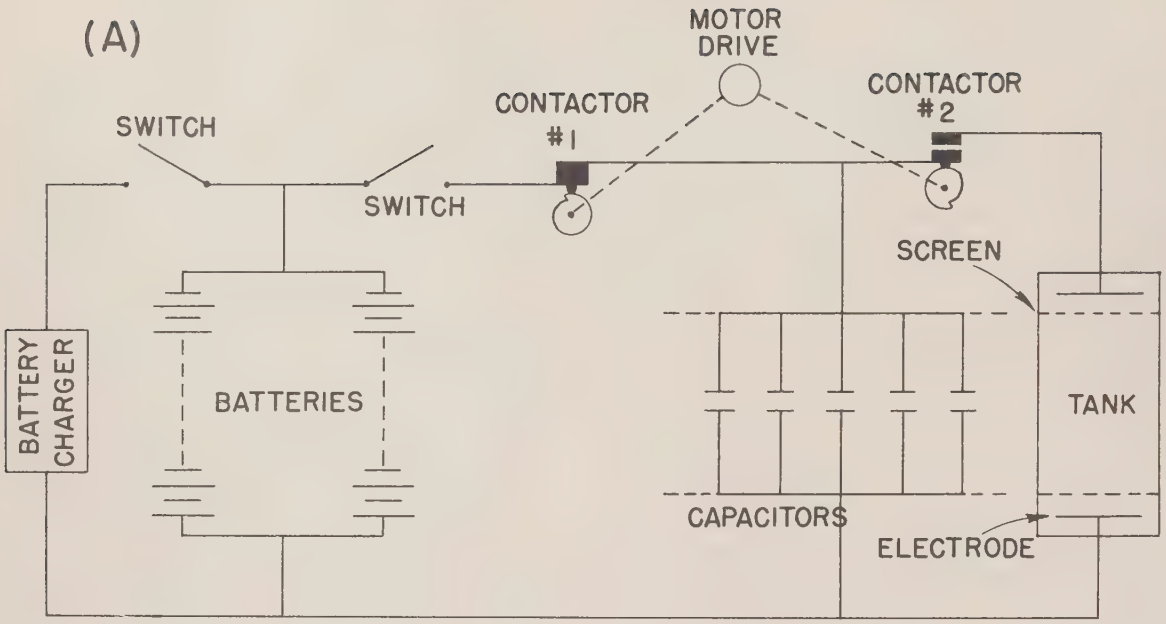
The discharge pulse is not, of course, a square wave, but rather an exponential decay as shown in figure 2B. McMillan et al. (1937) have shown that this exponential-decay pulse is equivalent in its physiological stimulus value to a square pulse of the same amplitude provided the duration of the square pulse is 37 percent of the time-constant of the decay-pulse. (The time-constant, T, of an exponential decay is the product RC, where R is the resistance of the discharge circuit in ohms and C is the capacity of the capacitor in farads.) Assuming that this relationship is applicable to the present situation, we can obtain an exponential-decay pulse equivalent to a 6-millisecond square pulse by letting $.37RC = .006$, where R is the resistance of the column of water between the electrodes, and C is then the required capacity. As $R = \rho\ell/A = 0.46$ ohms, C may be calculated at 0.035 farads, or 35,000 microfarads. This is an extremely large capacity, but in view of the low working voltage of about 60 volts, it is not a difficult capacity to obtain by means of banking small capacitors in parallel.

The charge and discharge cycle of the capacitor may next be considered. With a pulse frequency of 10 c.p.s., there is 0.1 second available for the entire cycle of charge and discharge corresponding to a single pulse. Now the time-constant, T, of this circuit is defined as the amount of time necessary for the current to decrease to 1/e of the original value, where $e \cong 2.72$ (the base of the natural logarithm). Thus, if the original current is 130 amperes, after a time T it will be $130/e = 48$ amperes, still too large a current to be broken by simple contacts. After a time 2T the current will be $48/e = 18$ amperes, and after a time 3T it will be $18/e = 6.5$ amperes. This current is sufficiently small to break by simple contacts without excessive arcing. So we see that, during the discharge, contacter No. 2 must stay closed for a period of time equal to two to three times the time-constant. The time-constant with the previously calculated values of R and C is 0.016 seconds. Three times this is 0.048 seconds, or slightly less than half of the cycle available for charging the capacitor. We have, then, 0.05 seconds to charge a capacity of 35,000 microfarads to a potential of 60 volts.

The resistance of the charging circuit, which includes the internal resistance of the batteries, must be sufficiently low so that the capacitor may become very nearly fully charged in this time. To satisfy this condition the batteries should be connected in series-parallel as shown in figure 4A and heavy connecting wires and terminals used.

An apparatus was constructed to approximate the requirements, as deduced above, to effect electrotaxis in tuna, 30 cm. or more in length, when confined in the large tank. The power source consisted of twenty 6-volt automobile storage batteries connected in series-parallel (two banks of 10 each). The power source (using any number up to 10 pairs of batteries) was used to charge a bank of fifty-five 1,000 mfd. (150 volt) capacitors connected in parallel to give a total capacity of 55,000 mfd. A motor-driven, variable-speed mechanical interrupter was constructed with two cams, 180° out of phase, operating two spring-loaded contact points (fig. 5).

The electric apparatus was connected by heavy electric cables to two plane electrodes (11 x 4 feet) fitted to each end of the tank, with a reversing switch included in the circuit. The electrodes, initially separated by a distance of 33 feet, consisted of a series of vertical copper wires soldered at intervals of 4 inches along a horizontal brass strip. The system was



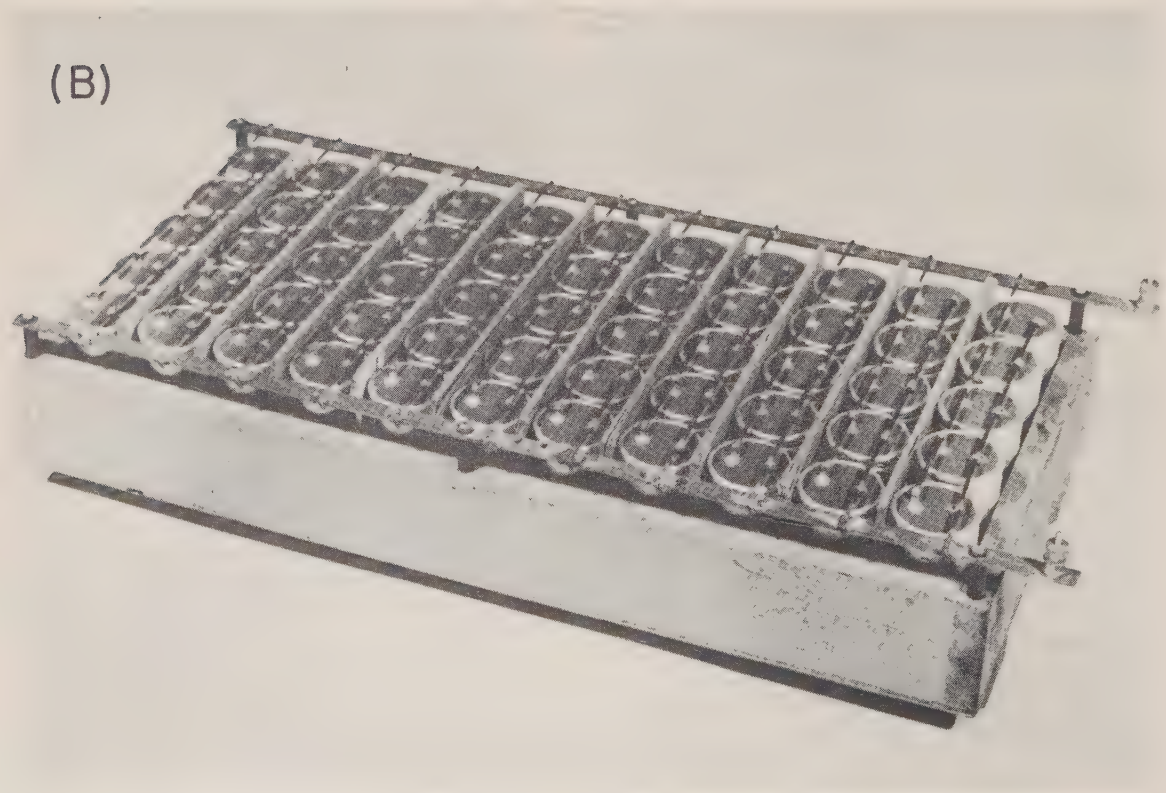


Figure 4.--The capacitor discharge circuit. A. Schematic diagram of complete system. B. Bank of fifty-five 1,000 mfd. capacitors.

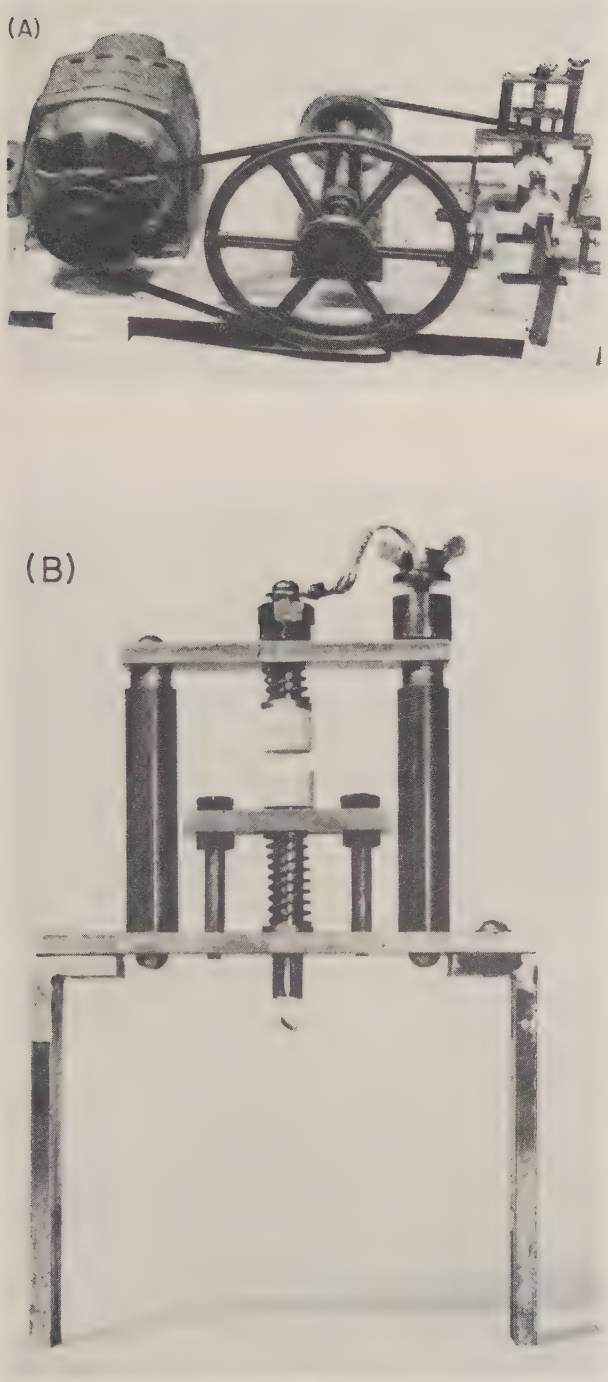


Figure 5.--The mechanical interrupter. A. General view showing variable speed motor, contactor (one is removed), and drive cams. B. Close-up view of spring-loaded contactor.

supported by a wooden framework and fronted by a plastic screen. To check the uniformity of the field, the potential was measured at regular intervals throughout the tank and the equipotential surfaces were determined. The electric field, which is normal to the equipotential surfaces, was very nearly uniform except for a slight distortion near the ends of the tank.

Procedure and Results

The experiments to be described below were made without any attempt at quantitative measurement of the response. Only a few fish were available; namely 1 jack or ulua (Caranx sp.), 2 dolphin or mahimahi (Coryphaena hippurus), 2 little tunny or kawakawa (Euthynnus yaito), and 3 yellowfin or ahi (Neothunnus macropterus). The fish were caught by trolling, transported to Coconut Island in the live well of the research vessel Salpa, and placed in the large 35 x 11 x 4-foot tank, which was supplied with running salt water (Tester 1952). The experiments are described in the order in which they were conducted.

The apparatus was initially tested on a jack about 50 cm. in length, with electrodes spaced a distance of 33 feet, with a source supply of 60 volts (2 banks of 10 batteries) and with a frequency of interrupters (capacitor discharge) of 10 per second. Without application of the field, the jack persisted in keeping to one corner of the tank, despite attempts to make it move around. This end of the tank was made negative. When the current was turned on, the fish was impelled rapidly to the positive electrode where it remained, bumping the protective screen, as long as the current persisted. When the current was turned off, the jack returned to its corner. This response would be classed as "perfect."

The test was repeated with the same source voltage but at a frequency of 1 c.p.s. There was still a good electrotactic response but the swimming movements were slower. Each pulse produced a strong muscular spasm. The same test was repeated a second time after an interval of a few minutes. This time narcosis began to set in and there was a loss of equilibrium. After the current was shut off the fish swam in an inverted position. A day or so later it died. Undoubtedly a satisfactory response could have been obtained with a lower source voltage.

In working with members of the tuna family it was more difficult to determine the effect of the current since these fish were in constant motion, swimming back and forth. The procedure generally followed with tunas was to turn on the current when the fish was swimming towards the

negative electrode and was near the middle of the tank. If there was any effect of the current then it should be most evident in such a position, since the fish would have to turn around and swim towards the positive electrode at a point where it would not ordinarily do so.

These tests were always started with a small voltage by connecting only a few batteries. The voltage was then increased in steps to the maximum of 60 volts, or to the point of satisfactory response.

The first of the tuna family to be tested was a 38-cm. little tunny. The interruption frequency was 10 per second. Up to 48 volts no effect was observed, but at 48 volts there was evidence of a slight annoyance, twitching, and a tendency to swim nearer to the surface. These were later found to be very typical symptoms for voltages too small to elicit electrotaxis. At 54 volts the fish swam normally for a moment and then suffered narcosis. The current was turned off at once. The fish sank to the bottom and lay motionless for about 5 minutes with only the gills moving slightly. Finally it started moving and soon swam off. After about a half-hour the fish began to bump into the sides of the tank and soon died. On the basis of later experiments this behavior was not typical of little tunny or other tunas and we have no explanation for this anomaly.

Following this, two dolphin (pelagic fish, but not of the tuna family) were tested successively. One was 67 cm. in length, and the other 61 cm. Neither orientation nor electrotaxis was noticed for any voltage up to the maximum at 10 c.p.s. Only the typical symptoms of annoyance, twitching, and swimming near the surface were observed. At 5 c.p.s. the response was even poorer.

The same results were obtained in the next two tests employing a 57-cm. little tunny and a 53-cm. yellowfin. The tests seemed to indicate, however, that decreasing the frequency below 10 per second resulted in a diminishing effectiveness in producing annoyance responses.

The next test was performed on a yellowfin of about 50-cm. length. The result was about the same as before with no indication of orientation or electrotaxis, but with some evidence that the higher frequencies were more stimulating than the lower.

It became evident that the tests would have to be extended to higher frequencies and greater field strengths. Moving the electrodes closer together was the only practicable method of increasing the field strength in the tank. The electrodes were then adjusted to a separation of 16 feet, thereby approximately doubling the maximum possible field strength.

The same yellowfin was tested under these new conditions. With maximum source voltage of 60 volts and an interruption frequency of 12 c.p.s., the fish immediately oriented towards the positive electrode and swam under the influence of the current until it hit the screen. The tuna would then continue to swim into the screen or along it and would bump into the side walls and even try to jump out. Under these conditions, then, very good electrotactic response was achieved.

Another yellowfin of approximately 50-cm. length was caught and placed in the tank with the yellowfin tested earlier. The test was then repeated with 60 volts at 12 c.p.s. The new fish also displayed satisfactory electrotaxis. At 16 c.p.s. and 60 volts the reaction was considerably more violent than at 12 c.p.s. With the voltage reduced to 48 volts the response was still satisfactory. Raising the frequency to 20 per second enabled the voltage to be reduced to 36 volts while maintaining satisfactory response. This frequency was the limit of the apparatus. Whether or not higher frequencies would allow even smaller voltages is unknown.

While in a state of electrotaxis the fish swam at the surface with its head partially out of the water, with mouth open wide, and with gill flaps extended. The last two yellowfin tested did considerable bumping into the screen and walls and occasionally showed signs of electronarcosis, but they continued to live for several weeks.

Discussion

In table 6 are shown the values of current density and electric field corresponding to the total applied voltages used in the foregoing experiments. A comparison with table 5 shows that the current densities and fields used with the tuna fall in the same range as those used with aholehole. But since the tunas were much larger fish than the aholehole the head-to-tail voltages produced by these fields were correspondingly greater for the tunas. For the third yellowfin tested the minimum head-to-tail voltage for satisfactory response was:

6.2 volts at 12 c.p.s.
4.9 " " 16 "
3.7 " " 20 "

Table 6.--The relationship between total applied voltage, current density, and electric field

Electrode spacing	Total voltage (V) volts	Current density (J), ma./cm.^{2}	Electric field (E), volts/cm.
33 ft.	48	2.6	0.048
	54	2.9	0.054
	60	3.2	0.060
16 ft.	36	4.0	0.074
	48	5.3	0.098
	60	6.4	0.12

Whereas with aholehole, the optimum response was obtained with 1 to 2 volts at 10 c.p.s.

The power dissipation per unit volume of water for the tests of the third yellowfin, cited above, was calculated to be as follows:

153 microwatts/cm.^{3} at 12 c.p.s.
131 " " 16 "
92 " " 20 "

These values are plotted in figure 6. The curve drawn is only one of many possible curves through the three points, but it seems highly improbable that the point at 20 c.p.s. could be at or near the minimum of the curve. The most likely possibility is that a minimum point in the curve occurs somewhere above 20 c.p.s. This question can be settled only by investigating the response of tuna at frequencies greater than 20 c.p.s.

It is interesting to look ahead to the possibility of testing this equipment in the open sea. Under these conditions and maintaining a similar spacing between electrodes, the total current would increase and hence the total power dissipation would also increase. This is a direct result of the tremendously greater cross-sectional area exposed between the electrodes when in the open sea.

In order to make an exact comparison of the power dissipated in each case one should go through a procedure similar to that in Appendix I, calculating the net resistance between two plane parallel electrodes in an infinite expanse of water. A useful approximation can be obtained simply by making use of the results as found in Appendix I for spherical electrodes.

Considering first the situation in the tank, the power dissipated by a d.c. voltage, V, connected to the electrodes would be $P = \frac{V^2}{R}$, where R is the resistance between electrodes and is given by $R = \rho \frac{L}{A}$ where ρ is the resistivity of the water, L is the distance between electrodes, and A is the cross-sectional area. Thus $P = \frac{V^2 A}{\rho L}$ is the power dissipated in the tank.

We shall now approximate the condition in the open sea by two spheres of radius (a), half submerged, spaced a distance (L) apart. In

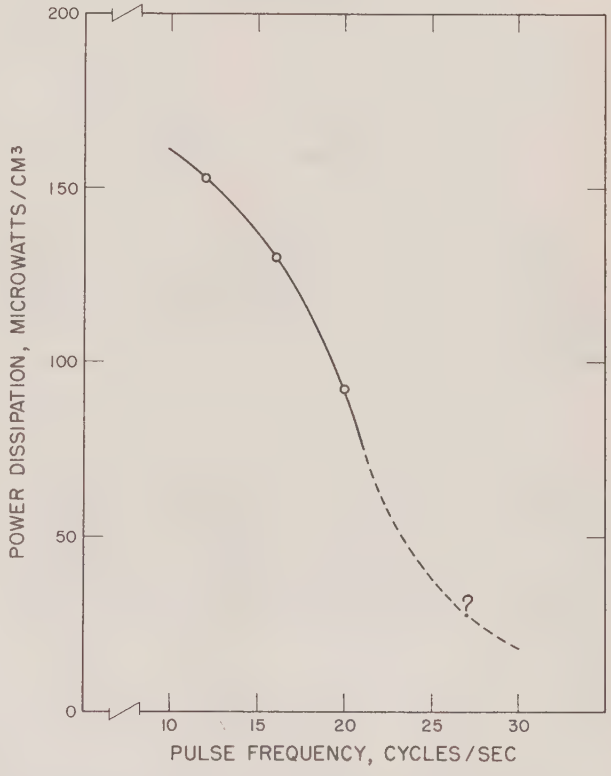


Figure 6.--Power dissipation per unit volume of water vs. pulse frequency for satisfactory response in tuna.

order to make this situation comparable to that in the tank we should have the same electric field strength midway between the two electrodes in each case. In the tank the field strength is $E = \frac{V}{L}$. In the case of the electrodes in the open sea, the field at the center is $E' = \frac{2aV_o}{d^2}$ where $2V_o = V'$ is the potential applied between the electrodes, and $d = \frac{L}{2}$. This is found from equation 14, Appendix I, by setting $r = 0$ and $\theta = 0$. Thus $E' = \frac{4aV'}{L^2}$ is the field midway between the electrodes in the open sea. If this is to be the same as in the tank we must set

$$E' = E$$

$$\text{or } \frac{4aV'}{L^2} = \frac{V}{L}$$

and $V' = \frac{VL}{4a}$ is the necessary relationship between the applied potentials for obtaining the same field midway between the electrodes.

The resistance between the open-sea electrodes is $R' = \frac{1}{\pi \sigma a} = \frac{\rho}{\pi a}$ ohms (eq. 23, Appendix I). Thus the power dissipation $P' = \frac{V'^2}{R'}$ becomes

$$P' = \left(\frac{VL}{4a}\right)^2 \frac{\pi a}{\rho}$$

The ratio of P' to P is now desired and is found from

$$P'/P = \frac{\left(\frac{VL}{4a}\right)^2 \pi a}{\frac{V^2 A}{\rho L}\rho} = \frac{\pi L^3}{16aA}$$

We must now assume values for L, a, and A. L was 16 ft. in the tank, and A was 44 sq. ft. Let us take $a = \frac{1}{20} L$ so that the approximations made in Appendix I will hold. Then a = 0.8 ft. These values give us

$$\frac{P'}{P} = \frac{\pi (16)^3}{16(0.8)(44)} = 23$$

Under the assumed conditions, then, 23 times as much power would be dissipated in the open sea as in the closed tank. Thus an apparatus of correspondingly higher power output would be required to effect electrotaxis in tuna at the same electrode spacing and frequencies.

SUMMARY

1. A theoretical study of the potential, electric field, and current density for spherical electrodes deeply submerged in a large body of water is included in Appendix I.

2. A theoretical study of the head-to-tail potential and current passing through a fish when immersed in fresh and salt water with a uniform electric field is included in Appendix II.

3. Preliminary experiments with aholehole in a small (12 x 2 x 2 feet) tank, using pulsed direct current with approximately square wave form indicated that the optimum frequency for electrotaxis was 10 c.p.s. and that the minimum peak current for satisfactory response (12 amperes) was associated with an on-fraction of 0.06 to 0.08. Total peak current requirements decreased with increase in length of the fish.

4. Extrapolating the above results, it was calculated that a current of 130 amperes at a potential of 60 volts would be required to induce electrotaxis in a 30-cm. fish in a tank of much larger size (35 x 11 x 4 feet). This was best achieved by capacitor discharge.

5. An apparatus was constructed for experiments with tuna and other large fish in the larger tank. It consisted of a bank of capacitors (55,000 mfd.) charged by two series banks of ten 6-volt automobile storage batteries and controlled by a variable speed mechanical contactor.

6. With this apparatus it was possible to induce electrotaxis in small (50-cm.) yellowfin tuna with electrodes spaced a distance of 16 feet. The electrotactic effect increased with pulse frequency up to 20 c.p.s., the maximum tested.

7. It was calculated that in the open sea 23 times as much power would be required to obtain an equivalent response with the electrodes spaced 16 ft. apart.

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APPENDIX I

THE ELECTRIC FIELD IN A CONDUCTING MEDIUM

When two metallic electrodes are placed in a body of water and a potential difference created between them, an electric field will be set up in all parts of the water, and a current will flow from one electrode to the other. The exact magnitude and direction of the electric field and current density at any point depend on the shape and location of the electrodes, and upon the boundary conditions of the conducting medium, the body of water. The solution of this problem in general is not easily amenable to mathematical analysis, but special electrode shapes and boundary conditions can be chosen which make possible a straightforward mathematical analysis. In such an analysis one must employ mathematically idealized conditions which as closely as possible approximate the actual conditions to be described.

In this instance the actual conditions to be described consist of two electrodes deeply submerged in a large body of water such as the ocean; the size of the electrodes is small (about 1/100th) compared to the distance between them, and the distance between the electrodes is small (about 1/100th) compared with the distance to any boundary (top, bottom, sides) of the body of water. These are conditions not difficult to satisfy in the open ocean.

The ideal conditions which closely approximate these actual boundary conditions may be taken as two metallic spheres of radius a as the electrodes, separated by a distance of $2d$ in a body of water of uniform conductivity σ and of infinite expanse in all directions. The solution of this ideal problem can then be taken as the solution of the actual problem with an error of less than 1 percent up to distances from the electrodes equal to about 10 times the electrode spacing.

We shall proceed, then, to solve the idealized problem. There are four things we wish to learn about this system: The electric field at any point in the medium, the current density at any point, the total current between electrodes, and the net resistance between the electrodes.

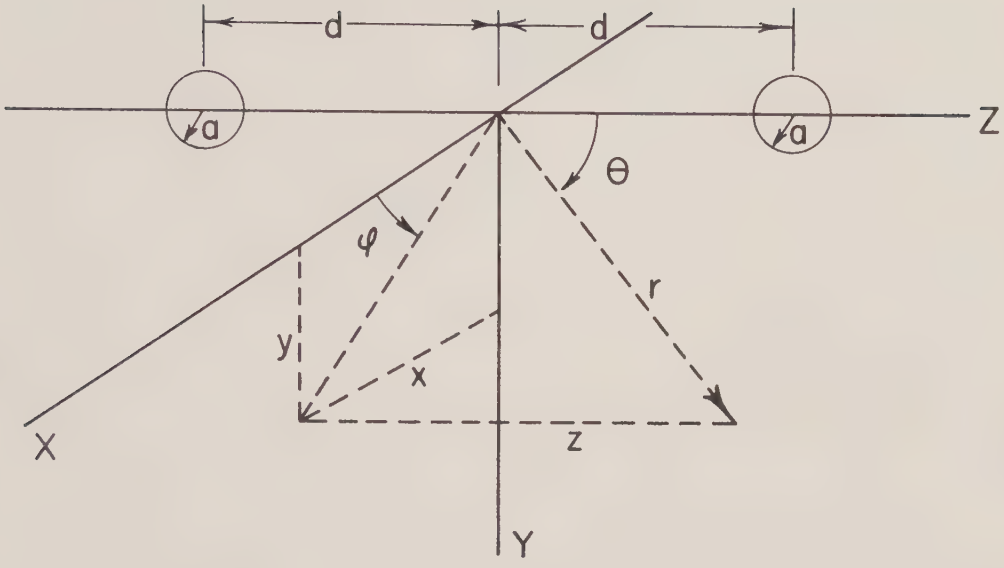
The approach to be used here will give the potential at any point in the medium. From this the electric field can be found by the relationship $\vec{E} = -\nabla V$, where $\vec{E}$ is the electric field (a vector quantity, having magnitude and direction), V is the potential (a scalar quantity), and ∇ is the vector differential operator which in Cartesian coordinates is given by $\nabla = \frac{\vec{i}\partial}{\partial x} + \frac{\vec{j}\partial}{\partial y} + \frac{\vec{k}\partial}{\partial z}$, and $\vec{i}$, $\vec{j}$, $\vec{k}$, are the unit vectors in the X-, Y-, and Z-directions respectively.

The current density is found by the relationship $\vec{J} = \sigma\vec{E}$, and the total current, I, is found by integrating the normal component of the current density over any surface completely enclosing one of the electrodes. The most convenient surface for this is the infinite plane which bisects and is normal to the line joining the two electrodes.

If one of the two electrodes is at a potential V_o and the other $-V_o$, then the total potential difference is $2V_o$. The net resistance between the two electrodes is then given by $R = \frac{2V_o}{I}$.

Let us take as the Z-axis of our coordinate system the line through the centers of the two electrodes, and the origin at the midpoint of the line joining the electrodes. Let the X-axis be directed horizontally, and the Y-axis vertically downward, as shown in the figure on the following page.

It is obvious that the field will be symmetrical about the Z-axis. This suggests that a spherical polar coordinate system might be the most convenient to use. In this system the coordinates of some point in space are given by r, θ, and φ, where r is the radial distance from the origin, θ is the angle between the radial line and the Z-axis, and φ is the angle between the projection of the radial line into the XY-plane and the X-axis. Since the field is symmetrical, it will depend only on the coordinates r and θ.



The Potential

The potential V at any point in the medium must satisfy Laplace's Equation $\nabla^2 V = 0$. Expanded, this is $\frac{\partial^2 V}{\partial x^2} + \frac{\partial^2 V}{\partial y^2} + \frac{\partial^2 V}{\partial z^2} = 0$ in Cartesian coordinates. The equivalent expression in spherical coordinates can be found from the transformation equations between the two coordinate systems:

$$r = [x^2+y^2+z^2]^{1/2}, \quad \theta = \tan^{-1}\frac{\sqrt{x^2+y^2}}{z}, \quad \varphi = \tan^{-1}\frac{y}{x}.$$

The result gives

$$\nabla^2 V = \frac{1}{r^2 \sin\theta}\left[\sin\theta \frac{\partial}{\partial r}\left(r^2 \frac{\partial V}{\partial r}\right) + \frac{\partial}{\partial \theta}\left(\sin\theta \frac{\partial V}{\partial \theta}\right) + \frac{1}{\sin\theta}\frac{\partial^2 V}{\partial \varphi^2}\right]. \tag{1}$$

We have already seen that V does not depend on φ. The last term, therefore, will be zero. The resulting equation is a partial differential equation for V in terms of r and θ.

The general solution of this equation is well known (MacRobert 1948) and is given in terms of the sum of an infinite series:

$$V = C_1\left[P_0 + rP_1 + r^2P_2 + r^3P_3 + \cdots\cdots\right]$$
$$+ C_2\left[\frac{1}{r}P_0 + \frac{1}{r^2}P_1 + \frac{1}{r^3}P_2 + \cdots\cdots\right]. \tag{2}$$

C_1 and C_2 are arbitrary constants that must be chosen so as to satisfy boundary conditions. The functions P_0, P_1, P_2, ... are functions of the angle θ known as Legendre Polynomials. They are defined as follows (Jahnke and Emde 1945):

$$P_n(u) = \frac{1}{2^n n!}\frac{d^n}{du^n}(u^2-1)^n, \quad n = 1, 2, 3, \cdots\cdots . \tag{3}$$

When $u = \cos\theta$, the first few polynomials are

$$P_0 = 1, \quad P_1 = \cos\theta, \quad P_2 = \frac{1}{4}(3\cos\theta + 1)$$
$$P_3 = \frac{1}{8}(5\cos 3\theta + 3\cos\theta), \quad P_4 = \frac{1}{64}(35\cos 4\theta + 20\cos 2\theta + 9)$$
$$P_5 = \frac{1}{128}(63\cos 5\theta + 35\cos 3\theta + 30\cos\theta) \tag{4}$$

The problem is now reduced to one of finding the boundary conditions to be satisfied by our solution. This is most easily arrived at by assuming that the field is being produced by electric charges +q at z = d and -q at z = - d. The magnitude of q must be such that the potential on the surface of the sphere of radius a surrounding the charge is V_o. Since the potential at any point in space due to a point charge is given by $V = \frac{q}{r}$, we see then that we must have $V_o = \frac{q}{a}$. Hence the magnitude of the charge is given by

$$q = V_o a. \tag{5}$$

We are neglecting here the interaction between the two charges since we have assumed that a << 2d.

For any point along the Z-axis beyond the point z = d, the potential is given by

$$V = \frac{q}{r-d} - \frac{q}{r+d}$$
$$= \frac{2dq}{r^2}\left(1 - \frac{d^2}{r^2}\right)^{-1}.$$

If the quantity $\left(1 - \frac{d^2}{r^2}\right)^{-1}$ is expanded in a Maclaurin series, we get

$$V = 2dq\left(\frac{1}{r^2} + \frac{d^2}{r^4} + \frac{d^4}{r^6} + \frac{d^6}{r^8} + \cdots\right), \quad r>d. \tag{6}$$

This expression is the boundary condition for the potential when $\theta = 0$ and $r > d$. For any value of θ and r, provided $r > d$, the solution is

$$V(r,\theta) = 2dq\left(\frac{1}{r^2}P_1 + \frac{d^2}{r^4}P_3 + \frac{d^4}{r^6}P_5 + \cdots\right), \quad r>d. \tag{7}$$

For any point along the Z-axis between z = 0 and z = d, the potential is given by

$$V = \frac{q}{d-r} - \frac{q}{d+r}$$
$$= \frac{2qr}{d^2}\left(1 - \frac{r^2}{d^2}\right)^{-1}.$$

Expanding again, we get

$$V = \frac{2qr}{d^2}\left(1 + \frac{r^2}{d^2} + \frac{r^4}{d^4} + \frac{r^6}{d^6} + \cdots\right), \quad r<d. \tag{8}$$

This expression is the boundary condition for the potential when $\theta = 0$ and $r < d$. For any value of θ and r, provided $r < d$, the solution is

$$V(r,\theta) = \frac{2q}{d^2}\left(rP_1 + \frac{r^3}{d^2}P_3 + \frac{r^5}{d^4}P_5 + \cdots\right), \quad r<d. \tag{9}$$

It is easily seen that equations (7) and (9) satisfy the boundary conditions (6) and (8) simply by setting $\theta = 0$ in the expressions $P_1, P_3, P_5 \ldots$. This gives $P_1 = P_3 = P_5 \ldots = 1$. Substitution of equations (7) and (9) into the differential equation (1) shows that they are indeed solutions.

We notice that the potential is given by one expression within the sphere of radius d, and another outside this sphere. Let us call the region outside the sphere of radius d the region 1, and the region inside the sphere region 2. To summarize our solution (setting $q = V_o a$) we have

$$V_1(r,\theta) = 2adV_o\left(\frac{1}{r^2}P_1 + \frac{d^2}{r^4}P_3 + \frac{d^4}{r^6}P_5 + \cdots\right) \text{ volts}, \quad r>d \tag{10}$$

$$V_2(r,\theta) = \frac{2aV_o}{d^2}\left(rP_1 + r^3P_3 + r^5P_5 + \cdots\right) \text{ volts}, \quad r<d \tag{11}$$

The Electric Field

The electric field is given by $\vec{E} = -\nabla V$. In spherical coordinates, when V is independent of φ, this becomes

$$\vec{E} = -\left[\vec{N}\frac{\partial V}{\partial r} + \vec{P}\frac{1}{r}\frac{\partial V}{\partial \theta}\right], \tag{12}$$

where $\vec{N} = \frac{\vec{r}}{|r|}$ is the unit vector in the radial direction, and $\vec{P}$ is the unit vector perpendicular to $\vec{N}$ in the direction of increasing θ. The partial derivatives are

$$\frac{\partial V_1}{\partial r} = 2adV_0\left(-\frac{2}{r^3}P_1 - \frac{4d^2}{r^5}P_3 - \frac{6d^4}{r^7}P_5 - \cdots\right)$$

$$\frac{\partial V_2}{\partial r} = \frac{2aV_0}{d^2}\left(P_1 + \frac{3r^2}{d^2}P_3 + \frac{5r^4}{d^4}P_5 + \cdots\right)$$

$$\frac{\partial V_1}{\partial \theta} = 2adV_0\left(\frac{1}{r^2}P_1' + \frac{d^2}{r^4}P_3' + \frac{d^4}{r^6}P_5' + \cdots\right)$$

$$\frac{\partial V_2}{\partial \theta} = \frac{2aV_0}{d^2}\left(rP_1' + \frac{r^3}{d^2}P_3' + \frac{r^5}{d^4}P_5' + \cdots\right)$$

where P_1', P_3', P_5', ... are the derivatives of P_1, P_3, P_5, ... with respect to θ (Jahnke and Emde 1945). Thus, the electric field in the two regions is given by

$$\vec{E}_1(r,\theta) = \vec{N}\left[2adV_0\left(\frac{2}{r^3}P_1 + \frac{4d^2}{r^5}P_3 + \frac{6d^4}{r^7}P_5 + \cdots\right)\right]$$
$$-\vec{P}\left[2adV_0\left(\frac{1}{r^3}P_1' + \frac{d^2}{r^5}P_3' + \frac{d^4}{r^7}P_5' + \cdots\right)\right] \text{ volts/cm., } r>d \tag{13}$$

$$\vec{E}_2(r,\theta) = -\vec{N}\left[\frac{2aV_0}{d^2}\left(P_1 + \frac{3r^2}{d^2}P_3 + \frac{5r^4}{d^4}P_5 + \cdots\right)\right]$$
$$-\vec{P}\left[\frac{2aV_0}{d^2}\left(P_1' + \frac{r^2}{d^2}P_3' + \frac{r^4}{d^4}P_5' + \cdots\right)\right] \text{ volts/cm., } r<d\ . \tag{14}$$

The Current Density

We have seen that the current density $\vec{J} = \sigma\vec{E}$, where σ is the conductivity of the medium. Thus the equations

$$\vec{J}_1 = \sigma\vec{E}_1 \text{ amperes/cm.}^2$$

$$\vec{J}_2 = \sigma\vec{E}_2 \text{ amperes/cm.}^2 \tag{15}$$

will give the current density at any point in the medium, with $\vec{E}_1$ and $\vec{E}_2$ defined by (13) and (14).

The current density on the perpendicular bisector plane, or the XY-plane, is found by setting $\theta = \frac{\pi}{2}$. At this angle the Legendre Polynomials have the values

$$P_1 = P_3 = P_5 = \cdots = 0$$

$$P_1' = -1,\ P_3' = 3/2,\ P_5' = -15/8,\ P_7' = 35/16, \ldots$$

Thus, the current density becomes

$$\vec{J}_1 = \vec{P}\left[2ad\sigma V_0\left(\frac{1}{r^3} - \frac{3d^2}{2r^5} + \frac{15d^4}{8r^7} - \frac{35d^6}{16r^9} + \cdots\right)\right] \text{ amp/cm}^2, \ r>d \tag{16}$$

$$\vec{J}_2 = \vec{P}\left[\frac{2a\sigma V_0}{d^2}\left(1 - \frac{3r^2}{2d^2} + \frac{15r^4}{8d^4} - \frac{35r^6}{16d^6} + \cdots\right)\right] \text{ amp/cm., } r<d \tag{17}$$

for points on the XY-plane. We notice that the current is everywhere in the direction of $\vec{P}$, which is a unit vector in the -Z direction when $\theta = \frac{\pi}{2}$.

The total current is found by integrating this current density over the entire XY-plane.

$$I = \iint J\,dA$$

where dA is the increment of area which in our case is $r dr d\varphi$. Thus

$$I = \int_d^\infty \int_0^{2\pi} J_1 r\, dr\, d\varphi + \int_0^d \int_0^{2\pi} J_2 r\, dr\, d\varphi = I_1 + I_2$$

The integration on φ simply yields the factor 2π. Then

$$I_1 = 4\pi\sigma a d V_0 \int_d^\infty r\left(\frac{1}{r^3} - \frac{3d^2}{2r^5} + \frac{15d^4}{8r^7} - \frac{35d^6}{16r^9} + \cdots\right) dr$$

$$= 4\pi\sigma a V_0 \left(1 - \frac{1}{2} + \frac{3}{8} - \frac{5}{16} + \frac{35}{128} - \cdots\right). \tag{18}$$

Likewise

$$I_2 = \frac{4\pi\sigma a V_0}{d^2} \int_0^d r\left(1 - \frac{3r^2}{2d^2} + \frac{15r^4}{8d^4} - \frac{35r^6}{16d^6} + \cdots\right) dr$$

$$= 4\pi\sigma a V_0 \left(\frac{1}{2} - \frac{3}{8} + \frac{5}{16} - \frac{35}{128} + \cdots\right). \tag{19}$$

Then

$$I = I_1 + I_2 = 4\pi\sigma a V_0 \left[\left(1 - \frac{1}{2} + \frac{3}{8} - \frac{5}{16} + \cdots\right) + \left(\frac{1}{2} - \frac{3}{8} + \frac{5}{16} - \frac{35}{128} + \cdots\right)\right].$$

We notice that the two infinite series are exactly the same, except for sign, after the 1 of the first series. Thus all terms cancel each other leaving only the term 1. Hence

$$I = 4\pi\sigma a V_0 \text{ amperes} \tag{20}$$

is the total current flowing between the two electrodes.

Resistance

The net resistance between the electrodes is the total applied potential divided by the total current.

$$R = \frac{2V_0}{I} = \frac{2V_0}{4\pi\sigma a V_0} = \frac{1}{2\pi\sigma a} \quad \text{ohms} \tag{21}$$

Discussion

It is to be noted that the problem is not essentially altered if the two electrodes are half submerged on the surface of an infinite body of water. The only changes will be in the total current and resistance. The total current will be one-half of the value in equation (20):

$$I = 2\pi\sigma a V_0 \text{ amperes} \tag{22}$$

and the total resistance will then be twice the value given in equation (21):

$$R = \frac{1}{\pi\sigma a} \text{ ohms.} \tag{23}$$

These conclusions are drawn from the fact that any plane through the Z-axis divides the field into two independent regions, for the electric field at all points in the plane is parallel to the plane. Thus, if one of the regions is air instead of water, it will not affect the behavior of the field and current in the other region.

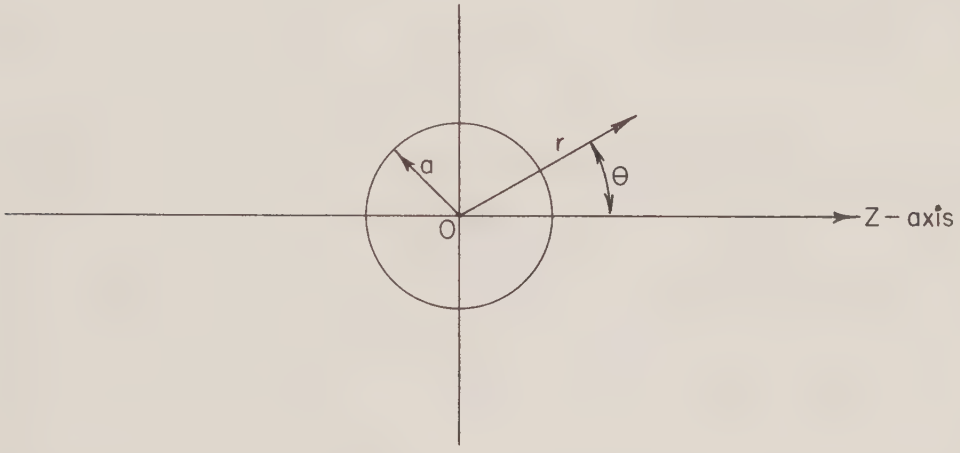
APPENDIX II

A FISH IN A UNIFORM ELECTRIC FIELD

We wish to analyze here the electrical problem of a fish located in a uniform electric field with the long axis of the fish parallel to the field. The problem is to determine the head-to-tail potential in the fish and the current through the fish.

In order to reduce this problem to mathematical analysis we must approximate the shape of the fish by some suitable geometrical model. A long, thin ellipsoid of revolution would approximate the shape of a fish very well, but would still leave the mathematical solution rather difficult. A simple model from a mathematical point of view is a sphere, and even though this is a rather poor model of a fish, the solution of this problem will at least give a qualitative answer to the original one.

We can assume that the uniform electric field is produced by two large, plane, parallel electrodes placed in the water with a wide separation as compared with the length of the fish. Let the strength of this uniform field be E_o. Let the conductivity of the water be σ_w and that of the fish (sphere) σ_f.



We shall choose the coordinate system so that the origin is at the center of the sphere of radius $\underline{a}$ and the Z-axis is in the direction of the field E_o. Any point inside or outside the sphere can then be designated by the polar coordinates $\underline{r}$ and $\underline{\theta}$. A third coordinate is not required since there is symmetry about the Z-axis.

The potential relative to the origin at any point inside or outside the sphere is found by the solution of Laplace's Equation

$$\frac{\partial}{\partial r}\left(r^2 \sin\theta \frac{\partial V}{\partial r}\right) + \frac{\partial}{\partial \theta}\left(\sin\theta \frac{\partial V}{\partial \theta}\right) = 0, \tag{1}$$

subject to the following boundary conditions:

a. The potential at the origin shall be taken as zero. Thus $V = 0$ at $r = 0$.

b. The field at large distances from the sphere must be equal to E_o. This requires that the potential at large distances be equal to $-E_o z$, where z is the coordinate along the Z-axis and $z = r\cos\theta$. Thus $V = -E_o r\cos\theta$ for large r.

c. The component of the current density normal to the surface of the sphere must be the same on both sides of the sphere. If E_f and E_w are the fields inside (in the fish) and outside the sphere (in the water) respectively, then $(E_f)_r$ and $(E_w)_r$ are the radial and hence normal components of these fields. This boundary condition then requires that $j_r = \sigma_f(E_f)_r = \sigma_w(E_w)_r$ at $r = a$, j_r being the normal component of the current density.

d. The inside and outside potentials must be equal on the surface of the sphere. Thus $V_f(r = a) = V_w(r = a)$.

In order to satisfy the boundary conditions, the solution of Laplace's Equation must be of the form

$$V_w = A_w r\cos\theta + \frac{B_w \cos\theta}{r^2} \tag{2}$$

outside the sphere, and so that boundary condition (a) is satisfied,

$$V_f = A_f r\cos\theta \tag{3}$$

inside the sphere. A_w, B_w, and A_f are constants to be determined by the boundary conditions.

At large distances from the sphere, eq. (2) becomes $V_w = A_w r\cos\theta$. According to boundary condition (b), at large distances $V = -E_o r\cos\theta$. Thus we see that $A_w = -E_o$.

The radial electric field is found by $E_r = -\frac{\partial V}{\partial r}$. Hence $(E_w)_r = -\frac{\partial V_w}{\partial r} = -E_o\cos\theta - \frac{2B_w\cos\theta}{r^3}$

$$(E_f)_r = -\frac{\partial V_f}{\partial r} = A_f\cos\theta.$$

According to boundary condition (c), these multiplied by σ_w and σ_f respectively must be equal at $r = a$. This gives

$$\sigma_f A_f = -\sigma_w E_o - \frac{\sigma_w 2B_w}{a^3}. \tag{4}$$

Equating the inside and outside potentials on the surface of the sphere as required by boundary condition (c) we obtain

$$A_f a = -E_o a + \frac{B_w}{a^2}. \tag{5}$$

Multiplying eq. (4) by a and eq. (5) by $-\sigma_f$, and adding, we obtain

$$0 = E_o a(\sigma_f - \sigma_w) - \frac{B_w}{a^2}(\sigma_f + 2\sigma_w).$$

Solving for B_w:

$$B_w = E_o a^3\left(\frac{\sigma_f - \sigma_w}{\sigma_f + 2\sigma_w}\right). \tag{6}$$

Substitution of this value of B_w into eq. (4) or (5) yields

$$A_f = -E_o\left(\frac{3\sigma_w}{\sigma_f + 2\sigma_w}\right). \tag{7}$$

The solution for the potential is thus

$$V_w = -E_o z\left(1 - \frac{\sigma_f - \sigma_w}{\sigma_f + 2\sigma_w}\frac{a^3}{r^3}\right) \tag{8}$$

$$V_f = -E_o z\left(\frac{3\sigma_w}{\sigma_f + 2\sigma_w}\right). \tag{9}$$

Head-to-tail Potential

The head-to-tail potential on the fish corresponds here to the potential difference between the points $z = a$ and $z = -a$. If the length of the fish is $L = 2a$, and the head-to-tail voltage is V_L, then

$$V_L = V_f(-a) - V_f(+a) = E_o L\left(\frac{3\sigma_w}{\sigma_f + 2\sigma_w}\right). \tag{10}$$

In other words, the head-to-tail voltage on a fish in a uniform electric field E_o is not merely its length times the field strength, but there is an additional factor depending on the relative conductivities of the fish and the surrounding water. In the special case where they are the same, $\sigma_f = \sigma_w$, then the factor reduces to 1. When the conductivity of the fish is greater than that of the water as could be

the case in fresh water, then $\sigma_f/\sigma_w > 1$. This means that

$$\left(\frac{3\sigma_w}{\sigma_f + 2\sigma_w}\right) = \left(\frac{3}{\sigma_f/\sigma_w + 2}\right) < 1$$

and the head-to-tail voltage in the fresh water is less than $E_o L$. When the surrounding medium is sea water $\sigma_f/\sigma_w < 1$ and the factor becomes greater than 1 so that the head-to-tail potential in sea water is greater than $E_o L$.

The electric field E_o is the field that must be applied to produce a given head-to-tail potential, V_L. From eq. (10) this field is

$$E_o = \frac{V_L}{L}\left(\frac{\sigma_f/\sigma_w + 2}{3}\right). \tag{11}$$

Thus, for a fixed V_L, the field E_o varies inversely with the length of the fish and the conductivity of the water.

These results are qualitatively correct but due to the crudeness of the model can give only a rough estimate of the magnitudes involved. If we assume a ratio of conductivity of sea water to fresh water of around 600, and the conductivity of fish intermediate between these two so that (σ_f/σ_w) sea = 1/25 and (σ_f/σ_w) fresh = 25, then the ratio of the electric fields required in sea and fresh water to produce the same head-to-tail potential on a given fish is

$$\frac{(E_o)\ \text{sea}}{(E_o)\ \text{fresh}} = \frac{1/25 + 2}{25 + 2} = \frac{2.04}{27} = 0.075.$$

Under these assumed conditions the field in sea water would therefore need to be about 1/10 as large as in fresh water.

Current Density

The current density in the fish is given by the product of the conductivity of the fish and the electric field in the fish, or $J_f = \sigma_f E_f$. But $E_f = -\frac{\partial V_f}{\partial z}$ so that

$$E_f = E_o\left(\frac{3\sigma_w}{\sigma_f + 2\sigma_w}\right).$$

Making use of equation (10) this is reduced to $E_f = V_L/L$. Thus

$$J_f = (\sigma_f/L)V_L. \tag{12}$$

The current density in the fish is a constant (σ_f/L) times the head-to-tail potential. These two parameters are therefore equivalent and neither one can be said to be responsible for the physiological response of the fish apart from the other.